X. *Some Remarks on* Heterogyna penella. By Thomas Algernon Chapman, M.D., F.E.S.

[Read March 16th, 1898.]

Heterogyna penella is a moth with an apterous female, and a male of the same flimsy black texture as many Psychids. But to these it does not appear to be at all related, nor to any other group with apterous females. Whether the very similar aspect of the males of *H. penella* and some Psychids is purely accidental, or whether habits similar in some respects are in any way facilitated by their very similar facies, that is, whether this black, gauzy texture is of advantage to both under like habits, is a question in elucidation of which I have not been able to range any facts.

Except that it is not of a whitish colour, the female of *H. penella* is more maggot-like than that of most Psychids. One of its most obvious differences is that it is coloured in almost exactly the same way as the larva, with a characteristic pattern in black and yellow, and it even happens, that a larva pale from a predominance of yellow, or dark from the dark markings being more pronounced produces a moth varying in precisely the same manner. The female moth has even been described as being the same as the larva, and superficially it resembles it very exactly. Besides the essential differences between a larva and an imago, it differs in possessing no appendages whatever; not only has it no wings and no legs, but it has no tubercles, scales, or hairs of any sort, the skin being smooth and shining, with some wrinkles due to muscular attachments and traces of circular marks in the position of the larval prolegs. The male moth even has some yellow markings on the abdomen that are in the same positions as those of the larva, these are actual body markings, the hairs being all black; though it is apparently clothed sparsely with hairs only, a considerable proportion of these, especially on the wings, are really scales, being somewhat flattened and striated.

The most specialised peculiarity of this moth (*H. penella* ♀) is that it emerges from its cocoon and pupa case, remains outside until the male is attracted and for a bare ten minutes after, and then re-enters its pupa case. This drops back into the cocoon, and the appearance is the same as if the moth had never emerged. The mechanism by which this manœuvre is accomplished by a maggot without appendages is very interesting.

Until last year (1897) I had never met with the species in sufficient numbers to make any observations of value; I had found the female pupa case a very puzzling structure, and not having seen the male pupa, could form no idea of its relationships. Last spring, however, I met with it freely at Digne and have been able to observe it very fully.

Whilst *Heterogyna penella* inhabits a large part of Southern Europe, it would appear that the Basses Alpes are its headquarters, and in some districts of this department it has even been described as destructive; it is not, therefore, surprising that Digne affords it in plenty, at an elevation of 2,000 to 3,000 feet. I do not think it is at all common towards the Mediterranean coast, but it descends to lower levels and a warmer climate than Digne, whilst I have also taken it at Lauteret at 8,000 feet, where intense cold obtains in winter, and the summer is comparatively short. Such a range of climate, with so narrow a geographical range is difficult to understand. As I am not aware that it is anywhere double brooded, I conclude that, in its warmer habitats, it goes into hibernation before midsummer.

The larva is full-fed at Digne about April 20th to 30th, at Lauteret nearer the end of June. The males are full-fed quite ten days before the females.

To spin their cocoons the males seek a dead twig of the food plant (chiefly broom at Digne) or a dry stem of grass, against one side of which, usually in a prominent and conspicuous position, they spin a spindle-shaped cocoon of silk, at first white, then turning golden-yellow, of a somewhat open texture, so that the contained larva or pupa is easily seen. A large proportion of these at once produce parasitic dipterous larvæ; only twice were any other parasites produced, these were chalcids.

The diptera emerge in confinement in six or eight weeks, certainly too early to infest the next brood of

penella, so doubtless they have alternative hosts, as with other of these dipterous parasites. I forwarded a small supply of them to Mr. Bignell, who attempted to ascertain their name, with the following results from different authorities:—*Demoticus plebeius*; a *Blepharidea* near *B. vulgaris*; a species of *Ceromasia*. For aught I know these are synonyms.

The female does not usually place her similar but much larger cocoon so conspicuously, and I think even makes some attempt to hide it, near the ground, under a leaf, &c., nor are so many to be seen, though the larvæ are equally abundant. These also produce the dipterous parasites, but I think much less abundantly than the males.

The larva in its short squat form and sluggish habits reminds one of those of the Zygænas, and like them they have minute stellate skin points. They retain, however, simple one-bristled tubercles up to the adult stage, and so have none of that angularity and upholstered-cushion appearance so characteristic of Zygænas.

The prolegs also, though of macro-lepidopterous type, are much less fully evolved than in the Zygænas. The circle of crochets is, indeed, quite incomplete on the outer aspect, but the hooks extend round the front and back of the pad suggesting rather a complete circle damaged on one side than the fully evolved foot with single inner flange of the Zygænas. The formula of the larval tubercles seems to be the same as that of the newly-hatched Zygæna. After the trapezoidals and supra-spiracular, we find a subspiracular, placed well below and slightly behind the spiracle, with three points placed in an equilateral triangle, of which two, an upper and an anterior, carry long hairs (IV and V), the third, below and behind, is merely a point; below this are two others (VI and VII) on the same level, half-way between the subspiracular and the prolegs (marginal). Of the larger larvæ the general skin surface is closely set with extremely fine hair-points, then there are numerous minute tubercles each carrying four to six short, apparently tubular bristles, these seem to be quite independent of the ordinary tubercles.

In the newly-hatched larva, the subspiracular tubercles are a posterior one, below but well behind the spiracle, and another rather lower and directly below the

spiracle, there is no trace of the third hairless point of the larger larva, nor of the tubercles being fused into one. The next tubercle is very low down, ventral rather than marginal, solitary, carrying one hair like the others. There is also a black plate on the dorsum of the second segment.

The female pupa is much less like the larva than the imago is. Anteriorly it resembles the larva, slightly obscured in colouring and with the head bent down in front of the thorax, and hardly a trace of true legs. The head is like that of the larva with the appendages dwindled and atrophied; the antennæ are conical prominences, and the labrum, labium and mandibles appear as slight projections. The bending forwards is really that of an ordinary pupa, a bending usually obscured by the presence of the wing- and leg-cases filling up the hollow in front. These anterior segments are quite soft and larva-like and may be regarded as free, though the pupa does not move. The terminal segments (5th to 10th abdominal) are enlarged, forming a rounded mass which makes the whole pupa look very like one of those toy tumblers that always stand upright on a hemispherical base. These posterior segments, unlike the anterior ones, are more of an ordinary brown pupal texture, but the larval markings are still visible, appearing to be deeply buried within them. It would not be correct to describe these segments as "fixed," since there are no incisions soldered together; the incisions are fully on the stretch and are of nearly the same texture as the rest of the segments. The spiracle of the first abdominal segment is of course fully exposed, there being no wings, and there are circular patches, as in the imago, marking the position of the ventral prolegs. The first thoracic spiracle cannot be detected; there is a point marking the position of the second. The spines on the anterior margins of the segments are microscopically small.

On emergence the pupa protrudes the head and several segments from the cocoon, and the pupal case opens by a slit beginning transversely behind the head, thence passing down each side to the third thoracic segment. This portion of the pupal case is very elastic, so that, as the moth emerges, the anterior and posterior flaps thus formed stretch forwards and backwards into a plane and, whilst the moth is outside, open widely something like the upper

and lower jaws of one of these reptiles whose gape is 180°. Their edges are smoothly continuous by the stretching of the material at their angle of union in the last thoracic segment, so that there is in fact no such angle or any danger of the slit continuing further down the pupa, the upper and lower sections being continuous, without any appearance of being separated by an open fissure or crack.

The moth when emerged retains an organic connexion with the pupa-case, and this is its most unusual feature. The imaginal legs, or rather the positions they should occupy, remain inseparable from the minute black papillæ that represent them in the pupa. If any attempt be made to separate the imago from the pupa case at this point, the pupal legs break away from the rest of the case, or more frequently, the separation is made at the expense of the imago, leaving bleeding wounds. The imaginal head continues also to occupy the pupal head; only twice have I seen it separated naturally, but it is not very difficult to extricate the head of the imago from that of the pupa. The imaginal head is almost identical with the pupal head, except that it is white and colourless and obviously not intended to be exposed, the antennæ and mouth parts existing as structureless elevations.

This, however, is not the only means by which the moth maintains its position. Organically connected with the anterior flap of the pupa case, the moth lies across the open mouth of the pupa, and its hinder extremity lies along the dorsal flap, formed of the dorsal thoracic segments. The ventral surface of the moth is swollen, so as exactly to fit the hollow these form in their inner surface, and there it adheres either by the suction of atmospheric pressure, or by an actual stickiness of the apposed surfaces. The bulb of the posterior segments of the pupa being still within the cocoon, the moth appears to be sitting across the mouth of the cocoon, the pupa case not being visible on a casual glance, though the moth is in contact with it throughout its whole ventral surface, except just centrally opposite the lumen of the chrysalis case. Fertilisation occupies five or ten minutes only, and this may be the whole duration of the imaginal existence outside its pupa case, since, as soon as this is accomplished, the moth commences to return into it and completes the process in about an equal time. Strong vermicular movements

reverse the process of emergence; these movements, however, pass backwards along the posterior surface and past the anal extremity, and forwards along the ventral surface. The full rounded extremity of the moth maintains its apposition with the dorsal jaw of the pupa case, which it glides along until it comes over the opening into the pupa case, into which it then goes by an ordinary vermicular movement.

The moth is thus replaced exactly into its former position in the pupa, the elastic jaws resuming their natural relations, and appearances are almost precisely as if the moth had never emerged. As a matter of fact, the dorsal plate of the prothorax overlaps the head, thus closing the opening more completely, but even so, a close examination is necessary to recognise the difference from an unemerged pupa.

The process of oviposition then commences and apparently lasts for some days, the denser bulbous part of the pupa case being packed with eggs, the moth acting as a stopper over them in the upper part.

Though little more than a bag of eggs, the female imago has a well-developed set of cutaneous muscles, in longitudinal, transverse and diagonal bundles, very much the same as may be demonstrated in the larva, and as are figured by Lyonet and others in the larvæ of other Lepidoptera.

The eggs are ovoid, yellow and delicate in texture, not unlike those of Zygænas and, like them, have a transparent space at one end. They do not appear to be laid in any particular order or arrangement, but adhere so firmly to each other and to the pupal shell, that any attempt to individualise them only results in smashing them. If exposed, as by breaking the chrysalis case and removing the moth, they very soon dry up and shrivel. A chief object, probably the chief object, of the remarkable modification of structure and economy in the female of *H. penella,* is evidently the protection of the ova from predaceous enemies and parasites, no doubt, but most especially from the danger of desiccation. That this is an object most necessary to be attained, will appear when we remember the high temperature and arid character of the country where the species is most plentiful, such as the neighbourhood of Digne. It seems to be very effectually carried out by the thick, elastic, gutta-percha-like texture

of the rounded posterior part of the pupa; brittle though this may be when its functions are completed and it is dried up, it is very tough and impervious whilst in use. Above, the moist body of the moth covers the eggs and is itself sheltered from evaporation by the anterior part of the pupa case. The cocoon again must prevent any very rapid circulation of air outside, and the eggs themselves form a dense solid mass.

Protection of the eggs against evaporation, or rather against desiccation, is a matter of imperative necessity for all insects in a hot and dry climate, and, indeed, under most circumstances. Usually, at least with our British Lepidoptera, this is secured by a position on or amongst herbage. Frequently laid on a leaf, the lower surface is thinner than the upper and absorbs moisture from the leaf as quickly as it evaporates from above. A very dense shell is another expedient, as in *Orgyia antiqua*, which has to exist for a long period, otherwise unprotected and unassisted. One advantage of the position in which the eggs of *Micropteryx* and Adelids are laid, viz., inside the plant tissues, is its moisture. One use, probably of the ribbing and flanging on the eggs of many butterflies and Noctuæ, is the impediment it offers to a rapid circulation of air over the egg surface, and those eggs that are enwrapped with hair and scales by the parent moth, benefit most from it, probably by the protection against desiccation so afforded. It is certainly not as a protection against cold, as its suggestion of blankets and swansdown at first makes us believe. It is not to hide them, since in most cases it makes them more conspicuous. It may be to make them more difficult of access to smaller foes, and unpalatable to larger ones. But no one who has tried to clean such an egg of its covering, and found how closely it is covered with scales and hair, and how difficult it often is to get a view of even a portion of egg shell after prolonged efforts to clean off the scales, can doubt that they must be very efficacious in preventing evaporation, both by their own thickness and that of the gum which attaches them so closely, and by their loose outer layers. Probably not a few of the less understood peculiarities of eggs have some reference to this protection.

Without denying that the protection provided in *H. penella* may be against enemies and parasites, as well as against drying up, it must be regarded as a remarkable

instance in having led to such extreme modifications of both the pupa and imago of the female moth and of her habits.

It is difficult to understand how the dispersal of the species is effected, and how a new area of its food plants gets colonised. The newly hatched larva is an excellent wanderer but is too small to cover any distance, and the older larva is very sluggish. What I have interpreted as a desire of the female larva to hide her cocoon, may be the result of some wandering that is instinctive at this period. Its chief resource for dispersion probably lies in the fact that it will eat almost anything papilionaceous and even other things, and so may manage to exist precariously across intermediate country.

When the young larvæ hatch they eat up the remains of their mother, leaving only a few fibrous shreds and some pellets, probably of urates. When emerged the moth does not void any ejecta or other fluid as nearly all insects do on exclusion, and the necessarily present effete material is no doubt represented by these pellets. The larvæ make their way out of the pupa case by the opening left in it, and also by forming some very small holes for themselves, but beyond this they make no attempt to eat the pupa case itself, which remains nearly uninjured. They are at first fairly active little wanderers, but are too small to travel any considerable distance; they feed readily, and Mr. W. H. B. Fletcher, to whom I sent some, tells me that when in their third skin they prepare for hibernation by forming a little cocoon, in size and form not unlike that of a *Nepticula*.

When we come to the male pupa, which presumably has not suffered any of these special adaptive modifications, we find that to be the case. There is nothing definite to distinguish it from one of *Zygæna*, except the very large antenna case, which overshadows the other appendage cases in front, and may be the reason why no femur case exists between the maxilla and first leg. It is black and shining, with abdominal segments 1 to 7 all free. The maxillæ are short, the antenna cases cover the second legs, the tips of the third legs project. The appendage cases extend to the end of the sixth abdominal segment. The pupa is deep from back to front about the seventh and eighth (third and fourth abdominal) segments, has a very marked waist (first abdominal seg-

ment) and tapers to the posterior extremity. The dorsal anterior margins of the abdominal segments are rough with longitudinal wrinkles on the fourth becoming very definite spines which on the later segments up to the eighth are placed two, three, and four deep, in irregular alternating rows. There is a certain amount of lateral flanging (as in *Zygæna* and *Procris*), that is, a soft wrinkled area leaves the harder parts in some degree as dorsal and ventral plates. In this flange some trace of the lateral yellow band of the larva still remains. The appendages are extremely polished and smooth, and are easily separated from each other. There is a large dorsal head piece, no trace of maxillary palpi; all seven abdominal spiracles are exposed.

For emergence the pupa projects from the cocoon through a loose valvular opening and remains there afterwards.

On dehiscence the eye pieces separate from the dorsal head pieces, and remain attached in front. In an empty pupa case the labrum, mandibles and well-developed labium are all very distinct.

In the male imago, the frenulum is interesting as consisting of a bundle of hairs, which are all separate at their bases, but unite into a solid bristle above; the frenulum has the appearance of being compounded in many species, but I do not remember it to have been actually resolved into its constituent hairs for a portion of its length in any other species I have observed.

The general surface of the wing-membrane is tinted as with a wash of indigo. In the forewing, a small portion at the base of the inner margin, corresponding with the jugum in the Jugatæ, is folded over on to the wing, the fold being clear of tinting and studded, as the rest of the wing is not, with very fine hairs. The corresponding portion of the hindwing is much larger, and is similarly marked off by a colourless line or area, from the base to the hind margin, where there is a notch.

The male pupa, the egg, larva and, I think, the imago all point to a close relationship to the Zygænidæ, but at a considerably lower level, as is chiefly evidenced by the larval tubercles and prolegs. The pupa also is probably lower, having the parts even less firmly soldered. Though one does not look to the female pupa for much light on the affinities of this form, owing to its being so specially

modified, it gives us, I think, this information, otherwise unattainable, that not only are all the forward abdominal segments "free," but the thoracic ones are so also. In the male pupa this is obscured by the appendages being partially soldered together, and fixing the body; but with the information obtained from the female pupa it may be inferred that we are correct in regarding the opening of the thoracic incisions on dehiscence as a proof that they are not fixed segments.

The resemblance to Psychids appears to be entirely superficial. The Psychids are clearly derived from a Tineid stirps and have a pupa associated with many Tineids in its amount of specialisation. Assuming a relationship of *H. penella* to Psychids, then it must have branched off before *Psyche* left *Tinea*, *i.e.*, before it had made the first steps to a vermiform female, before in fact it was a *Psyche*. On the other hand, the larval prolegs show that *Heterogyna* has been an external feeder, at least, for a long time, and in this respect it is as much above *Psyche*, as pupally it is beneath it. In other words, we have to go a long way outside the Psychids to find a common point of relationship; or, in the usual way of expressing such a degree of relationship, there is no relationship at all, that is beyond their both being somewhat generalised forms in many respects.